NeoBiota 47: 81–94 (2019)
doi: 10.3897/neobiota.47.35000
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Comparative feeding behaviour of native and introduced terrestrial snails tracks their ecological impacts

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Academic editor: *J. Jeschke* | Received 29 March 2019 | Accepted 10 May 2019 | Published 20 June 2019

Citation: Hoxha T, Crookes S, MacIsaac I, Chang X, Johansson M, Dick JTA, Nicolai A, MacIsaac HJ (2019) Comparative feeding behaviour of native and introduced terrestrial snails tracks their ecological impacts. NeoBiota 47: 81–94. https://doi.org/10.3897/neobiota.47.35000

Abstract

A developing body of theory and empirical evidence suggest that feeding behaviour as measured by the functional response (FR) can assist researchers in assessing the relative potential, ecological impacts and competitive abilities of native and introduced species. Here, we explored the FRs of two land snails that occur in south-western Ontario, one native (*Mesodon thyroidus*) and one non-indigenous (*Cepaea nemoralis*) to Canada. The non-indigenous species appears to have low ecological impact and inferior competitive abilities. Consistent with theory, while both species conformed to Type II functional responses, the native species had a significantly higher attack rate (5.30 vs 0.41, respectively) and slightly lower handling time (0.020 vs 0.023), and hence a higher maximum feeding rate (50.0 vs 43.5). The non-indigenous species exhibited a significantly longer time to contact for a variety of food types, and appeared less discriminating of paper that was offered as a non-food type. The non-indigenous species also ate significantly less food when in mixed species trials with the native snail. These feeding patterns match the known low ecological impact of the introduced snail and are consistent with the view that it is an inferior competitor relative to the native species. However, field experimentation is required to clarify whether the largely microallopatric distributions of the two species in south-western Ontario reflect competitive dominance by the native species or other factors such as habitat preference, feeding preferences or predator avoidance. The relative patterns of feeding behaviour and ecological impact are, however, fully in line with recent functional response theory and application.

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Keywords
Alien species; functional response; interspecific competition; non-indigenous species

Introduction

Introduction of non-indigenous species (NIS) is largely a consequence of unintentional and intentional human-mediated mechanisms. Once introduced, some NIS adversely affect native species and alter the communities in which they establish (e.g. Dick et al. 2017a). Elton (1958) proposed that characteristics of a native community could be important in providing resistance by native species against successful establishment of NIS. A large literature subsequently demonstrated that interactions (largely predation and competition) by native species could impair or prevent establishment of NIS (e.g. Levine et al. 2004; Smith-Ramesh et al. 2017), though the opposite may also occur (e.g. Levine et al. 2004; Cobián-Rojas et al. 2018). However, the specific mechanisms and thus the predictability of such species interactions and their outcomes remains poorly studied.

Numerous researchers have explored the role of interspecific competition in invasion ecology and its impacts on native ecosystems (e.g. Paini and Roberts 2005). Cases in which a native species competitively excludes a potential invader are particularly interesting, as they may provide valuable insights into context-specific factors that permit the native species to resist invasion (Paini et al. 2008; Zenni and Nuñez 2013). In many other cases, colonizing species may suppress native ones or limit their distributions (e.g. Petren and Case 1996).

One promising method of studying the possible impacts of NIS and the role of interspecific competition is through the use of the "functional response" (FR; see Dick et al. 2017b). Originally developed to study predator–prey relationships, FRs represent the relationship between resource consumption rate and resource density (Holling 1959). Indeed, competition theory refers to the "functional resource utilization response" of competing plant species (Tilman 1977). Using comparative FRs, Xu et al. (2016b) revealed that the impact of the invasive apple snail *Pomacea canaliculata* in relation to native *Bellamya aeruginosa* and introduced *Planorbius corneus* was predictable from the method. Similarly, comparative FRs were used to highlight the strong ecological impact of the "killer shrimp" *Dikerogammarus villosus* on native *Gammarus pulex* (Dodd et al. 2014). Thus, FRs can be used to assess impact on shared resources and hence relative competitive ability of native species and actual or potential invaders with respect to their resource uptake rates (Dick et al. 2017a). In particular, however, this method can move from understanding to predicting invasive species impacts (Dick et al. 2014).

Cepaea nemoralis is a terrestrial snail introduced to North America from its native Western Europe (Örstan and Cameron 2015). Its ornamental value and colourful appearance are responsible for its intercontinental spread by humans (Whitson 2005). The species occupies a wide variety of habitats and can be found in parks and gardens within cities (Ożgo 2012), but does not appear to have significantly harmful effects once introduced (Cowie et al. 2009; Ożgo and Bogucki 2011). This is the case

in Windsor and Essex County, Ontario, Canada, where *C. nemoralis* populations are abundant, particularly in urban and disturbed areas. Despite its commonness in these environments, it is rarely found in largely undisturbed woodlands of the region. It is possible that its absence from undisturbed woodlands is at least partly explained by the presence of the native snail *Mesodon thyroidus*, a similarly-sized species found mainly in woodlands including Kopegaron Woods Conservation Area (KWCA), where it often occurs on or in downed logs or under leaf litter. Preliminary surveys of KWCA confirmed the presence of *C. nemoralis* in the more disturbed forest periphery, but the two species never co-occurred in the interior of the forest.

A recent review indicated a significant role of olfaction in detection and selection of food by many terrestrial gastropods, though its importance varies by species (Kiss 2017). It is not clear whether the FRs of species are affected by olfaction nor whether interactions between native species and NIS could be influenced by it.

In this study, we address multiple aspects of the foraging ecology of these two terrestrial snail species, specifically their functional responses, odour detection capabilities and possible interspecific competition. We hypothesized that native, forest-inhabiting *M. thyroidus* may competitively exclude *C. nemoralis* from this habitat type. Specifically, we hypothesized that *M. thyroidus* would exhibit a greater attack rate, shorter handling times (and thus greater maximum feeding rate), shorter search times during olfactory tests, and greater consumption of limited resources in joint foraging experiments with the introduced snail. These predictions follow comparative FR and feeding theory (Dick et al. 2014). To test our hypotheses, we thus used a functional response (FR) framework to compare resource acquisition parameters (i.e. attack rate and handling time) for both these herbivorous snails. We also conducted odour detection experiments to determine whether olfactory cues were important to either species when locating food. Finally, we conducted joint foraging microcosm experiments to observe the relative competitive ability of both snails when placed in a confined environment with limited resources.

Methods

Native *Mesodon thyroidus* snails were found on wooden logs and leaf litter and hand-picked from the ground in KWCA in Leamington, Ontario, Canada, during July 2016. Non-native *Cepaea nemoralis* snails were collected from various urban areas of downtown Windsor, Ontario. Each species was separately housed in transparent aquarium tanks that were covered with fish net mesh to allow oxygenation while preventing egress of snails. Both tanks were maintained in a light- and temperature-controlled chamber (16:8 light:dark regime at 21 °C). Food for snails consisted mainly of grasses, maple leaves (*Acer* sp.) and dandelion leaves (*Taraxacum officinale*) obtained near the Great Lakes Institute for Environmental Research (GLIER), Windsor, Ontario. Snails were fed *ad libitum* during the acclimation period. Dechlorinated water was added to both tanks daily to maintain humidity.

Functional response experiments

Experimental food consisted of dandelion (*Taraxacum officinale*), which is a non-native species in both habitats occupied by the snail species. Dandelion has been used in previous feeding experiments with gastropods (e.g. Desbuquois and Daguzan 1995; Hanley et al. 2003, 2018). Preliminary feeding trials demonstrated that both snail species consumed dandelion, though Hanley et al. (2018) determined that dandelion seedling contained anti-herbivore phenolics and alkaloids and were only moderately acceptable as food to snails (*Cornu aspersum*) in feeding trials.

Snails were used for functional response (FR) experiments following a 24 h food deprivation period to standardize hunger levels. Each FR trial lasted 24 h as preliminary trials showed negligible food consumption over shorter (4 h) periods. Transparent boxes (7.6 × 11.4 cm) were used as arenas to hold food and snails during experiments. A grid composed of 1.3 cm squares was fixed below the box to form a 54-square base (6 × 9). Experimental dandelion leaves were hole-punched to produce circular pellets of uniform diameter (7 mm) as food for the snails. Pellets were placed in the centre of each square to standardize distance between adjacent food items. Original pellets (n = 2) were placed at the centre of the box along the short axis, and subsequent food levels (4, 8, 12, 16, 20, 24, 28, 32, 42, 54) were achieved by adding symmetrically along this axis (i.e. non-randomly).

To begin the experiment, adult and subadult snails were placed at the centre of the arena. Five trials were conducted at each food level for the native *M. thyroidus* and six for the introduced *C. nemoralis*. The arena was uniformly sprayed with deionized water to provide moisture, and boxes were covered with a lid during the trials. At the end of the test period, dandelion consumption was recorded. An event was recorded as full consumption if at least half a pellet was consumed; partial consumption (<50%) was not recorded. Species' FRs were calculated as described below.

Odour detection experiments

Odour preference experiments were conducted in single-species trials with one randomly selected snail individual each. *Mesodon thyroidus* ranged between 1.27 and 2.87 g, whereas *C. nemoralis* ranged between 0.48 and 3.50 g. Fresh dandelion pellets (formed as above) were subjected to one of four treatments: a) desiccation in an oven at 40 °C for 24 h; b) freezing at 0 °C for 24 h; c) pellets from freshly picked leaves; and d) pellets of the same shape but consisting of white paper as a negative control. Freezing significantly reduces volatility of odour compounds in leaves, while oven-drying may cause these compounds to be preserved (Díaz-Maroto et al. 2002). We recorded pellet consumption (as above) for each pellet density (2, 4, 8, 16) and pellet type. We placed a black barrier in the middle of the arena between the pellets and the snail to obstruct its view of the pellets and thereby limited detection by olfactory cues. Time to first contact of a prey item was recorded for each treatment. Each trial was conducted for four hours and repeated with five snails of each species for all food treatments. Species were tested separately (i.e. non-choice experiments).

Joint foraging experiments

The arenas described above for the FR trials were also used to test for possible competition between native and non-native snails. Trials were conducted with a 16:8 light:dark regime at 21 °C. Food pellets hole-punched from dandelion leaves were individually placed in separate squares of the arena (densities 2, 4, 8, 16, 32, 54). Pellets were placed at the centre of the arena and added symmetrically along the short axis of the arena (i.e. successively out to the arena wall as food density increased). For each pellet density tested, five individuals from each species were starved 24 h prior to the trials. We then placed individual native and non-native snails at opposite corners of the shorter edge of the arena facing the pellets. During the 4 h observation, consumed pellets were not replaced, and the number of pellets consumed (defined above) by each snail was recorded.

Data analysis

Statistical analyses were performed in R-3.5.0 (R Core Team 2018). To analyze and model comparative functional responses, we used the FRAIR-0.5.100 package (Pritchard 2017). Rogers' (1972) Type II equation was used to describe the functional response of both species as food resources were not replaced as they were consumed:

$$N_e = N_o(1 - \exp(a(N_e h - T)))$$

where N_e is the number of food pellets consumed, N_o is the initial number of food pellets, a is attack rate, h is handling time, and T is experimental duration (which was set at 1 in the present study as we wished to compare FR parameters for both species over the same period of time). Maximum feeding rate was thus calculated as 1/h. Models were bootstrapped (n = 2000) to generate 95% confidence intervals for each species' functional response curve. Species differences in attack rate (a), handling time (h) and maximum feeding rate ($1/h$) were analyzed using frair_compare() option within the FRAIR-0.5.100 package. Here, as the time for feeding was the same for both species and set as 1 above, a and h were used as unitless, comparative metrics consistent with many previous studies (e.g. Paterson et al. 2015; Anderson 2016; Pritchard et al. 2017), though other researchers have applied units (e.g. Rall et al. 2012, Lefébure et al. 2014, Li et al. 2018). In the latter case, attack rate (a) refers to the volume or area searched per unit time by a consumer, whereas handling time (h) refers to the time spent per unit of resource in activities such as capturing, subduing, killing, ingesting and digesting that resource unit (Barrios-O'Neill et al. 2016; Li et al. 2018).

To compare differential responses to food treatments and delineate interactions of independent variables in the odour detection experiments, we conducted an ANCOVA analysis with factors Species and Food Treatment and continuous variable Food Density, and their interactions. From 160 total observations, 52 instances in which individuals made no contact with the food (regardless of treatment type) were omitted. Nine other instances were also removed from the analysis: four cases

in which technical/equipment difficulties caused delays in recording time to pellet contact, four in which snails partially consumed the barrier intended to limit detection to olfactory cues, and one where the barrier became damaged from repeated use and was unable to fully hide the pellets. Detection times were $Log_{10}(x+1)$-transformed prior to analysis.

Results from joint foraging experiments were analyzed with a paired *t*-test by examining pellet consumption by each snail species across each of the six resource level classes. Each food class was represented five times.

Results

Both snail species conformed to a Type II functional response, though *C. nemoralis* has not reached the curve's asymptote and *M. thyroidus* individuals exhibited a significantly greater feeding ability with increasing food levels (Fig. 1). There was no overlap in 95% CIs, indicating substantially higher feeding efficiency and rate for the native compared to the introduced snail (Figure 1). *M. thyroidus* had a significantly greater attack rate (a = 5.30) than *C. nemoralis* (a = 0.41) (z = –9.97, P < 0.001), as well as a slightly shorter but non-significantly different handling time (h = 0.020 versus 0.023; z = 0.25, P = 0.800). Corresponding maximum feeding rate was higher for the native species (50.0 vs 43.5 pellets over the experimental time; see Fig. 1, Table 1).

Mean food detection times for native *M. thyroidus* (1585 s, SE = 369 s) across treatments were shorter than for non-indigenous *C. nemoralis* (1970 s, SE = 266 s). $Log_{10}(x+1)$-transformed detection times for food resources were significantly shorter for *M. thyroidus* than for *C. nemoralis* (ANCOVA, $F_{1,83}$ = 9.10, P < 0.01). This was the case for all treatments, with the exception of the "paper" treatment, where *M. thyroidus* took longer to detect the pellets on average (3937 s) than *C. nemoralis* (2094 s). Food density was also significant ($F_{1,83}$ = 7.27, P < 0.01), as average detection times generally decreased with increasing food density for all but one food level (n = 8 pellets). Furthermore, food treatment types differed significantly in detection times ($F_{3,83}$ = 4.02, P < 0.05) (Table 2), with "paper" averaging the longest time to detection (2764 s) and oven-dried foods the shortest (1334 s). Time to first contact was also affected by a species*food treatment interaction ($F_{3,83}$ = 3.19, P < 0.05) (Fig. 2).

The joint species foraging experiments demonstrated that feeding activity of *M. thyroidus* was significantly higher than that of *C. nemoralis* across a variety of food resource levels (paired *t*-test, t = 4.2, df = 29, P < 0.001) (Fig. 3).

Table 1. Rogers' Type II Functional Response parameters (± SE) for native (*M. thyroidus*) and non-native (*C. nemoralis*) snails, including attack rate (a), handling time (h), and maximum feeding rate ($1/h$).

Species	a	h	Maximum feeding rate ($1/h$)
Mesodon thyroidus	5.30 (0.49)	0.020 (<0.01)	50.0
Cepaea nemoralis	0.41 (0.05)	0.023 (0.01)	43.5

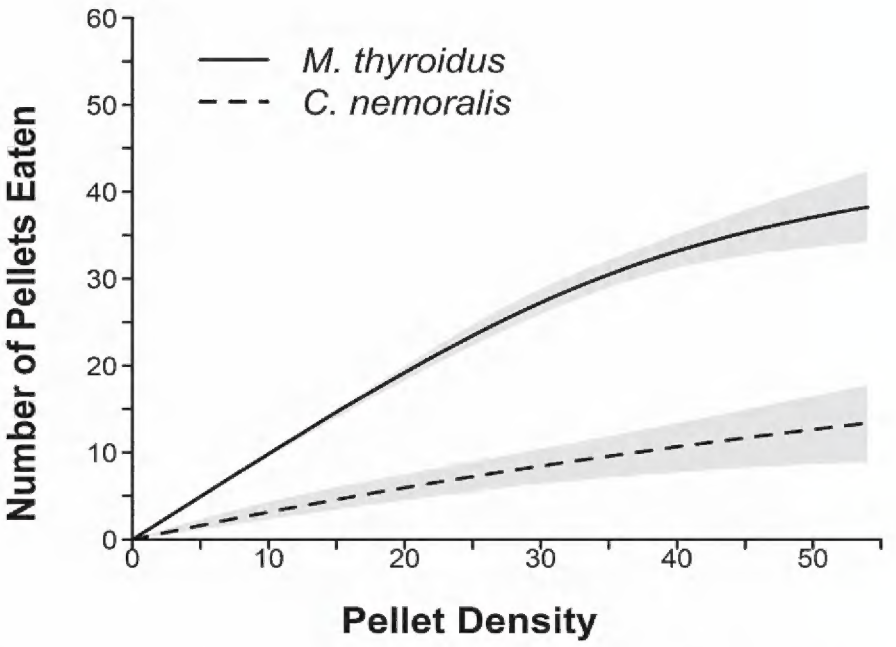

Figure 1. Fitted functional response curves of native *M. thyroidus* (solid line) and introduced *C. nemoralis* (dashed) with 95% CI bands (grey).

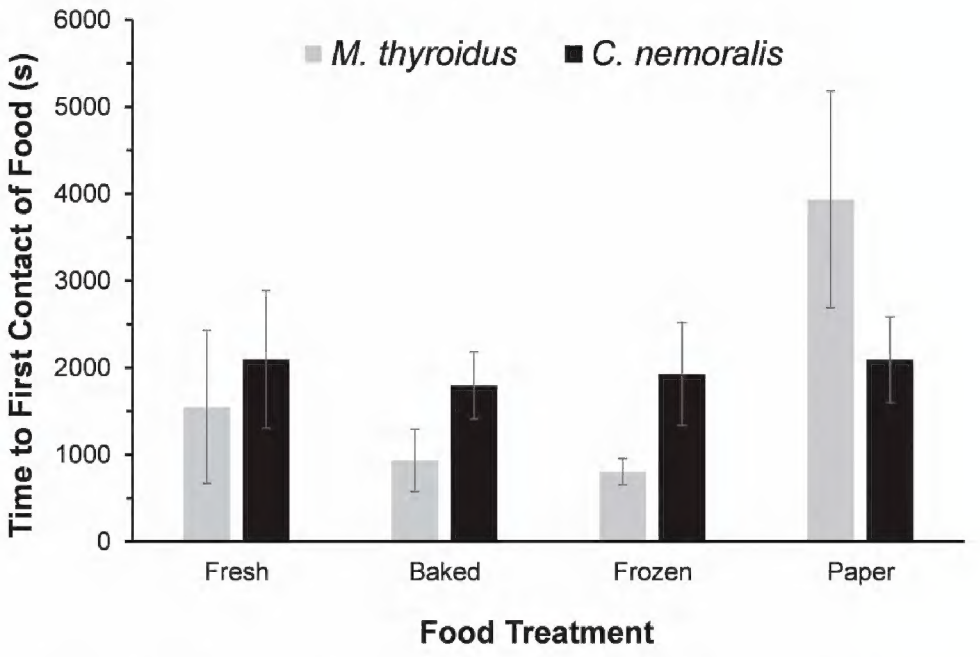

Figure 2. Mean (± SE) food detection times of native *M. thyroidus* (gray) and introduced *C. nemoralis* (black) snails across different food treatments.

Table 2. Results of ANCOVA test assessing effect of Species, Density, and Food Treatment on detection time from the olfaction experiment.

	df	F value	P
Species	1	9.1	0.0034
Density	1	7.3	0.0085
Treatment	3	4.0	0.0100
Species*Density	1	1.7	0.2026
Species*Treatment	3	3.2	0.0280
Density*Treatment	3	1.2	0.3300
Species*Density*Treatment	3	0.2	0.9022
Residuals	83		

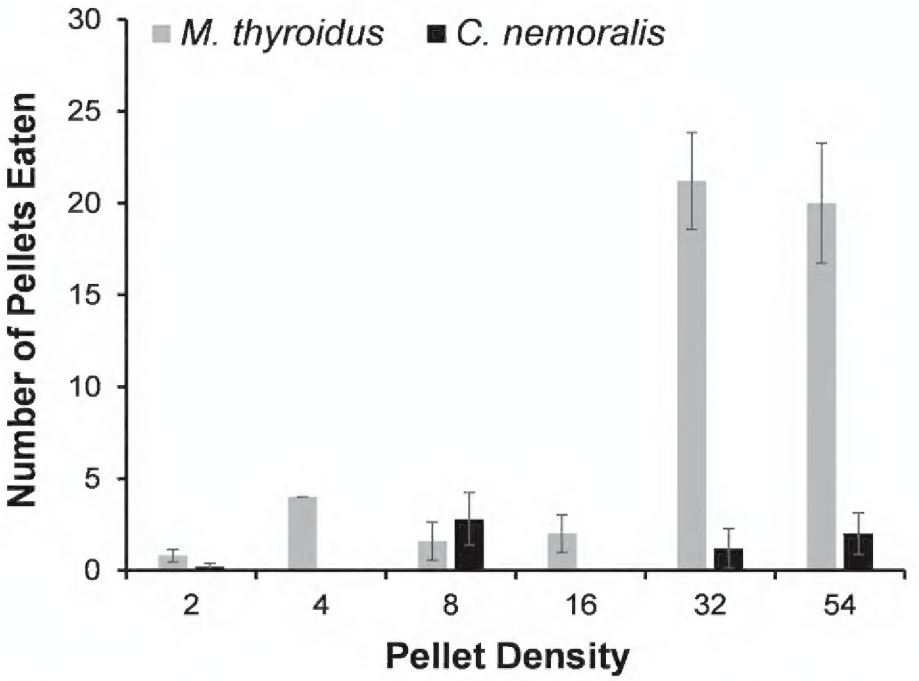

Figure 3. Mean (± SE) pellets eaten in joint foraging experiments across increasing food levels by native *M. thyroidus* (gray) and introduced *C. nemoralis* (black) snails.

Discussion

Application of comparative functional responses has allowed researchers to discriminate between invader species with high and low ecological impact (e.g. Dick et al. 2014, 2017a; Xu et al. 2016b), and may elucidate relative competitive ability (Tilman 1977; Dick et al. 2017b). In most cases examined to date, high functional responses of invaders (relative to their native counterparts) are associated with high ecological impact (Dick et al. 2017a); the opposite pattern is expected with low impact non-indigenous species. Bollache et al. (2008) proposed that the method could be used for NIS likely to invade, thereby allowing forecasts of comparative impact of a putative invader with a complementary native analogue. Further, Dick et al. (2017b) argued that, as with plant competition (see Tilman 1977), FRs of animals may uncover relative interspecific competitive abilities. In our study, we thus examined functional responses of native *M. thyroidus* and introduced *C. nemoralis* snails that occur in different habitats in south-western Ontario. In line with theory, we observed higher FRs for the native species, a consequence mainly of its higher attack rate and maximum feeding rate. The native snail also had a shorter time to first contact across different food densities. The native snail did, however, have a longer time to contact with non-food (i.e. paper pellets), suggesting it is more discriminating than the introduced snail. Indeed, the native species exhibited much shorter times to contact with actual food than with paper, whereas no such variation was apparent with the introduced species (Fig. 2). These experimental outcomes are consistent with the introduced snail having low (or at least unremarkable) ecological impact (see Cowie et al. 2009; Ożgo and Bogucki 2011). This supports general FR theory (Dick et al. 2014), that high FRs are associated with high ecological impact, and vice versa, that low FRs should be associated with low ecological impact. Our data also suggest that the native species is the superior

resource competitor, again consistent with FR theory (see Dick et al. 2014, 2017a). In particular, the higher attack rate of the native is congruent with competition theory, as superior competitive ability is likely to be exhibited by the competitor that can best utilise food resources at low food abundance (Tilman 1977), and attack rate quantifies this (see Fig. 1). This also is consistent with the hypothesis that the native species exerts some degree of biotic resistance toward the non-indigenous species.

The two snail species used in our study were collected from separate but nearby habitats. There exist many possible reasons for non-overlapping habitat use by species including interspecific differences in habitat preference and environmental tolerance (e.g. Moreno-Rueda 2007; Książkiewicz et al. 2013), or predation and its avoidance (Morris 2003; Green et al. 2011). It is also possible that non-overlapping distributions could result from intense interspecific competition, with species segregating into different habitats to minimize competition or exploit different resources (Cowie and Jones 1987; Kimura and Chiba 2010). Baur and Baur (1990) demonstrated that land snails competed via both exploitative and interference competition, while Parent and Crespi (2009) proposed that interspecific competition constrained phenotypic variation in Galapagos land snails. However, Chiba and Cowie (2016) found only limited support for exploitation or interference competition among land snail species. Experimental field work is required to assess the respective roles of habitat preference or biological interactions in the microallopatric distributions of these two snail species in south-western Ontario. In addition, molecular analyses of gut contents may improve our understanding of overlap in resource use by these and other species (Waterhouse et al. 2014).

Snail feeding behaviour has been well studied in both terrestrial and marine environments. Much of the recent focus on feeding pertains to mechanisms of food detection, particularly olfaction (e.g. Dahirel et al. 2015; Kiss 2017; Cordoba et al. 2018). To date, only a limited number of studies have addressed functional responses of land snails (see Broekhuizen et al. 2002; Haubois et al. 2005; Giacoletti et al. 2016; Xu et al. 2016a, 2016b; Pusack et al. 2018). In our laboratory study, both native and introduced species conformed with a Type II functional response, consistent with previous studies (e.g. Xu et al. 2016a, 2016b; Pusack et al. 2018). Type II curves are important from the context of population regulation of the resource, as relative risk to prey increases as prey density declines, destabilizing the interaction (Dick et al. 2014). Our study highlighted significantly higher feeding rates by the native snail versus the introduced one, consistent with field patterns of low invader impact and low competitive ability. At the other extreme, Xu et al. (2016b) observed that a highly ecologically damaging invasive snail had much higher feeding rates than its native counterpart. Thus, the FR method is able to predict degree of ecological impact and competitive ability, particularly if combined with species abundances, and can be used to both understand current invasions and forecast the outcome of emerging and future invasions (Dick et al. 2014, 2017b).

Our study utilized a categorical system to assess pellet consumption. One limitation of this approach was that feeding could be assessed as complete when it was only partial, or nonexistent even though some herbivory occurred (<50%). In addition, our results

were potentially affected by trial duration (1 d). Had the duration of these trials been extended (e.g. 2 d), some of the observations in the latter category may have flipped from "non-consumption" to total consumption. Finally, it is important to recognize that our study was conducted with only one invasive and one native species (the only species available) and that differences obtained only demonstrate species differences. Confirmation that these differences were due to the origin of the species would require tests with additional species. However, our data and case study fit closely with current FR theory and, together with these numerous other cases (see Dick et al. 2017a), show great potential in predicting ecological and competitive impacts from benign to highly damaging.

Moving forward, further studies of the context-dependency of snail species impacts should focus on mapping FRs onto impact under different contexts, such as various temperature and humidity regimes that might be expected with climate change. In addition, as invaders with low FRs may still exert ecological impact due to high abundance (see Dick et al. 2017b), the impact of native and invasive snails needs to be monitored as relative and absolute abundances change.

Acknowledgements

We thank Muaaz Tariq for assistance with animal husbandry and experimental setup. We appreciate helpful comments from Drs Gregor Kalinkat and Jonathan Jeschke and an anonymous reviewer. TH was supported by NSERC Undergraduate Scholarship, HJM by NSERC Discovery Grant and Canada Research Chair, and XC and HJM by a Joint Grant of Yunnan Provincial Science and Technology Department - Yunnan University Major Project (2018FY001-007).

References

Anderson TL (2016) Predation risk between cannibalistic aeshnid dragonflies influences their functional response on a larval salamander prey. Journal of Zoology 300: 221–227. https://doi.org/10.1111/jzo.12376

Barrios-O'Neill D, Kelly R, Dick JTA, Ricciardi A, MacIsaac HJ, Emmerson MC (2016) On the context-dependent scaling of consumer feeding rates. Ecology Letters 19: 668–678. https://doi.org/10.1111/ele.12605

Baur B, Baur A (1990) Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. Journal of Animal Ecology 59: 301–315. https://doi.org/10.2307/5174

Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. Biology Letters 4: 166–169. https://doi.org/10.1098/rsbl.2007.0554

Broekhuizen N, Parkyn S, Miller D, Rose R (2002) The relationship between food density and short term assimilation rates in *Potamopyrgus antipodarum* and *Deleatidium* sp. Hydrobiologia 477: 181–188. https://doi.org/10.1023/A:1021011225513

Chiba S, Cowie RH (2016) Evolution and extinction of land snails on oceanic islands. Annual Review of Ecology, Evolution, and Systematics 47: 123–141. https://doi.org/10.1146/annurev-ecolsys-112414-054331

Cobián-Rojas D, Schmitter-Soto JJ, Betancourt CMA, Aguilar-Perera A, Ruiz-Zárate MA, González-Sansón G., Monteagudo PPC, Pavón RH, Rodríguez AG, Wong RIC, Guerra DC, Torres HS, Valderrama SP (2018) The community diversity of two Caribbean MPAs invaded by lionfish does not support the biotic resistance hypothesis. Journal of Sea Research 134: 26–33. https://doi.org/10.1016/j.seares.2018.01.004

Cordoba M, Millar JG, McDonnell R (2018) Development of a high-throughput laboratory bioassay for testing potential attractants for terrestrial snails and slugs. Journal of Economic Entomology 111: 637–644. https://doi.org/10.1093/jee/tox377

Cowie RH, Dillon Jr RT, Robinson DG, Smith JW (2009) Alien non-marine snails and slugs of priority quarantine importance in the United States: a preliminary risk assessment. American Malacological Bulletin 27: 113–132. https://doi.org/10.4003/006.027.0210

Cowie RH, Jones JS (1987) Ecological interactions between *Cepaea nemoralis* and *Cepaea hortensis*: competition, invasion but no niche displacement. Functional Ecology 1: 91–97. https://doi.org/10.2307/2389710

Dahirel M, Cholé H, Séguret A, Madec L, Ansart A (2015) Context dependence of the olfactory perceptual range in the generalist land snail *Cornu aspersum*. Canadian Journal of Zoology 93: 665–669. https://doi.org/10.1139/cjz-2015-0001

Desbuquois C, Daguzan J (1995) The influence of ingestive conditioning on food choices in the land snail *Helix aspersa* Muller (Gastropoda: Pulmonata: Stylommatophora). Journal of Molluscan Studies 61: 353–360. https://doi.org/10.1093/mollus/61.3.353

Díaz-Maroto M, Pérez-Coello M, Cabezudo M (2002) Effect of different drying methods on the volatile components of parsley (*Petroselinum crispum* L.). European Food Research and Technology 215: 227–230. https://doi.org/10.1007/s00217-002-0529-7

Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions 16: 735–753. https://doi.org/10.1007/s10530-013-0550-8

Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Britton JR, Medoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017a) Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54: 1259–1267. https://doi.org/10.1111/1365-2664.12849

Dick JTA, Alexander ME, Ricciardi A, Laverty C, Downey PO, Xu M, Jeschke JM, Saul W-C, Hill MP, Wasserman RJ, Barrios-O'Neill D, Weyl OLF, Shaw RH (2017b) Functional responses can unify invasion ecology. Biological Invasions 19: 1667–1672. https://doi.org/10.1007/s10530-016-1355-3

Dodd JA, Dick JT, Alexander ME, MacNeil C, Dunn AM, Aldridge DC (2014) Predicting the ecological impacts of a new freshwater invader: functional responses and prey selectivity

of the 'killer shrimp', *Dikerogammarus villosus*, compared to the native *Gammarus pulex*. Freshwater Biology 59: 337–352. https://doi.org/10.1111/fwb.12268

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen, London, 181 pp. https://doi.org/10.1007/978-1-4899-7214-9

Giacoletti A, Rinaldi A, Mercurio M, Mirto S, Sara G (2016) Local consumers are the first line to control biological invasions: a case of study with the whelk *Stramonita haemastoma* (Gastropoda: Muricidae). Hydrobiologia 772: 117–129. https://doi.org/10.1007/s10750-016-2645-6

Green PT, O'Dowd DJ, Abbott KL, Jeffery M, Retallick K, MacNally R (2011) Invasional meltdown: invader-invader mutualism facilitates a secondary invasion. Ecology 92: 1758–1768. https://doi.org/10.1890/11-0050.1

Hanley ME, Bulling MT, Fenner M (2003) Quantifying individual feeding variability: implications for mollusc feeding experiments. Functional Ecology 17: 673–679. https://doi.org/10.1046/j.1365-2435.2003.00779.x

Hanley ME, Shannon RWR, Lemoine DG, Sandey B, Newland PL, Poppy GM (2018) Riding on the wind: volatile compounds dictate selection of grassland seedlings by snails. Annals of Botany 122: 1075–1083. https://doi.org/10.1093/aob/mcy190

Haubois AG, Guarini JM, Richard P, Fichet D, Radenac G, Blanchard GF (2005) Ingestion rate of the deposit-feeder *Hydrobia ulvae* (Gastropoda) on epipelic diatoms: effect of cell size and algal biomass. Journal of Experimental Marine Biology and Ecology 317: 1–12. https://doi.org/10.1016/j.jembe.2004.11.009

Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist 91: 293–320. https://doi.org/10.4039/Ent91293-5

Kimura K, Chiba S (2010) Interspecific interference competition alters habitat use patterns in two species of land snails. Evolutionary Ecology 24: 815–825. https://doi.org/10.1007/s10682-009-9339-8

Kiss T (2017) Do terrestrial gastropods use olfactory cues to locate and select food actively? Invertebrate Neuroscience 17: 9. https://doi.org/10.1007/s10158-017-0202-2

Książkiewicz Z, Kiaszewicz K, Goldyn B (2013) Microhabitat requirements of five rare vertiginid species (Gastropod, Pulmonata: Vertiginidae) in wetlands of western Poland. Malacologia 56: 95–106. https://doi.org/10.4002/040.056.0207

Lefébure R, Larsson S, Bystrom P (2014) Temperature and size-dependent attack rates of the three-spined stickleback (*Gasterosteus aculeatus*); are sticklebacks in the Baltic Sea resource-limited? Journal of Experimental Marine Biology and Ecology 451: 82–90. https://doi.org/10.1016/j.jembe.2013.11.008

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7: 975–989. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Li Y, Rall BC, Kalinkat G (2018) Experimental duration and predator satiation levels systematically affect functional response parameters. Oikos 127: 590–598. https://doi.org/10.1111/oik.04479

Moreno-Rueda G (2007) Refuge selection by two sympatric species of arid-dwelling land snails: different adaptive strategies to achieve the same objective. Journal of Arid Environments 68: 588–598. https://doi.org/10.1016/j.jaridenv.2006.08.004

Morris DW (2003) Toward an ecological synthesis: a case for habitat selection. Oecologia 136: 1–13. https://doi.org/10.1007/s00442-003-1241-4

Örstan A, Cameron RAD (2015) *Cepaea nemoralis* in Burlington, New Jersey, USA: Its possible origin and state 157 years after its introduction. Journal of Conchology 42: 193–198.

Ożgo M (2012) Shell polymorphism in the land-snail *Cepaea nemoralis* (L.) along a west-east transect in continental Europe. Folia Malacologica 20: 181–253. https://doi.org/10.2478/v10125-012-0015-1

Ożgo M, Bogucki Z (2011) Colonization, stability, and adaptation in a transplant experiment of the polymorphic land snail *Cepaea nemoralis* (Gastropoda: Pulmonata) at the edge of its geographical range. Biological Journal of the Linnean Society 104: 462–470. https://doi.org/10.1111/j.1095-8312.2011.01732.x

Paini DR, Funderburk JE, Reitz SR (2008) Competitive exclusion of a worldwide invasive pest by a native. Quantifying competition between two phytophagous insects on two host plant species. Journal of Animal Ecology 77: 184–190. https://doi.org/10.1111/j.1365-2656.2007.01324.x

Paini DR, Roberts JD (2005) Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (*Hylaeus alcyoneus*). Biological Conservation 123: 103–112. https://doi.org/10.1016/j.biocon.2004.11.001

Parent CE, Crespi BJ (2009) Ecological opportunity in adaptive radiation of Galápagos endemic land snails. The American Naturalist 174: 808–905. https://doi.org/10.1086/646604

Paterson RA, Dick JTA, Pritchard DW, Ennis M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: a community module functional response approach reveals context dependencies. Journal of Animal Ecology 84: 453–463. https://doi.org/10.1111/1365-2656.12292

Petren K, Case TJ (1996) An experimental demonstration of exploitation competition in an ongoing invasion. Ecology 77: 118–132. https://doi.org/10.2307/2265661

Pritchard DW (2017) frair: Tools for Functional Response Analysis. R package version 0.5.100. https://CRAN.R-project.org/package=frair

Pritchard DW, Paterson PA, Bovy HC, Barrios-O'Neill D (2017) FRAIR: an R package for fitting and comparing consumer functional responses. Methods in Ecology and Evolution 8: 1528–1534. https://doi.org/10.1111/2041-210X.12784

Pusack TJ, White JW, Tillotson HG, Kimbro DL, Stallings CD (2018) Size-dependent predation and intraspecific inhibition of an estuarine snail feeding on oysters. Journal of Experimental Marine Biology and Ecology 501: 74–82. https://doi.org/10.1016/j.jembe.2018.01.005

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Rall BC, Brose U, Hartvig M, Kalinkat G, Schwarzmüller F, Vucic-Pestic O, Petchey OL (2012) Universal temperature and body-mass scaling of feeding rates. Philosophical Transactions of the Royal Society B 367: 2923–2934. https://doi.org/10.1098/rstb.2012.0242

Rogers D (1972) Random search and insect population models. Journal of Animal Ecology 41: 369–383. https://doi.org/10.2307/3474

Smith-Ramesh LM, Moore AC, Schmitz OJ (2017) Global synthesis suggests that food web connectance correlates to invasion resistance. Global Change Biology 23: 465–473. https://doi.org/10.1111/gcb.13460

Tilman D (1977) Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58: 338–348. https://doi.org/10.2307/1935608

Waterhouse BR, Boyer S, Wratten SD (2014) Pyrosequencing of prey DNA in faeces of carnivorous land snails to facilitate ecological restoration and relocation programmes. Oecologia 175: 737–746. https://doi.org/10.1007/s00442-014-2933-7

Whitson M (2005) *Cepaea nemoralis* (Gastropoda, Helicidae): the invited invader. Journal of the Kentucky Academy of Science 66: 82–88. https://doi.org/10.3101/1098-7096(2006)66[82:CNGHTI]2.0.CO;2

Xu M, Dick JTA, Ricciardi A, Fang M, Zhang CY, Gu DG, Mu XD, Luo D, Wei H, Hu YC (2016a) Warming mediates the relationship between plant nutritional properties and herbivore functional responses. Ecology and Evolution 6: 8777–8784. https://doi.org/10.1002/ece3.2602

Xu M, Mu X, Dick JTA, Fang M, Gu D, Luo D, Zhang J, Luo J, Hu Y (2016b) Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. PLoS ONE 11(1): e0147017. https://doi.org/10.1371/journal.pone.0147017

Zenni RD, Nuñez MA (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. Oikos 122: 801–815. https://doi.org/10.1111/j.1600-0706.2012.00254.x